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Diet and Trophic Niche of Two Sympatric *Physalaemus* Species in Central Brazil

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Abstract. Given the increasing use of sympatric species to investigate niche differentiation and resource partition in biological communities, our study analyzes diet composition differences and trophic niche overlap between the sympatric species *Physalaemus cuvieri* and *P. atim* in the municipalities of Silvânia and Leopoldo Bulhões, Brazil. We used stomach flushing to obtain stomach contents from each individual and identified 11 prey categories for *P. cuvieri* and 17 for *P. atim.* Isoptera had the highest proportional volume in both species. No difference was found in the mean prey volume per stomach. Detrended correspondence analysis distribution scores indicated a greater diet breadth for *P. atim* than *P. cuvieri,* which is consistent with a higher trophic niche breadth in *P. atim* than *P. cuvieri.* According to a multi-response permutation procedure analysis, *P. cuvieri* and *P. atim* have different diet compositions. Our findings suggest that these congeneric species occupy sufficiently different dietary niches to enable them to persist in sympatry.

Keywords. Anurans; Cerrado; Food items; *Physalaemus atim;* Segregation.

INTRODUCTION

Ecologists have applied sympatric species models seeking to understand species coexistence and community structure by investigating niche differentiation and resource partitioning in biological communities. Coexistence of sympatric species derives from coevolution through their process of adapting to a habitat by avoiding competition with reduced overlap of resource use regarding at least one niche dimension (Leibold and McPeek, 2006). Thus, spatial and temporal dimensions as well as food availability are regarded as the most important factors in niche differentiation (Pianka, 1974; Schoener, 1974).

Many studies have found differences in the trophic niches of sympatric species of tropical anurans, including findings on food resource overlap (e.g., de Paula-Lima et al., 2010; Sabagh et al., 2012; Oliveira et al., 2015) and identification of food resource partitioning in prey size, feeding time period, and predator size classes (e.g., Lima and Magnusson, 1998; Menin et al., 2005). These studies are useful to determine ecological differences of closely related species.

Physalaemus Fitzinger, 1826 is one of the most speciose genera of Leptodactylidae Werner, 1896 (1838), with 48 recognized species widely distributed throughout South America, including from the Guianas, the lowlands of southern Venezuela, the llanos of southeastern Colombia, western Ecuador, Bolivia, Paraguay, Uruguay, northern and central Argentina, and Brazil (Nascimento et al., 2005; Lourenço et al., 2015; Frost, 2020). Brazil harbors 44 species of *Physalaemus* (Frost, 2020). *Physalaemus cuvieri* Fitzinger, 1826 is widely distributed throughout South America, while *P. atim* Brasileiro and Haddad, 2015 has been recorded only in the municipalities of Campo Limpo de Goiás (type locality) and Terezópolis de Goiás (Brasileiro and Haddad, 2015; Frost, 2020). Distributions of both species overlap in central Brazil, with sympatry in open Cerrado areas of Goiás state. Detailed studies on the diet of *P. cuvieri* have been carried out in some localities (Moreira and Barreto, 1996; Becker et al., 2007; Araújo et al., 2009; Menin et al., 2015; Leivas et al., 2018), but no studies on the diet of *P. atim* have been conducted.

Our study provides information on the diet and trophic niche overlap of *Physalaemus cuvieri* and *P. atim* in aquatic habitats of open Cerrado areas in central Brazil and report on (1) the diet composition of the species at the study site and (2) the food niche overlap between them. *Physalaemus* species are morphologically, behaviorally, and phyloge-

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netically similar, which suggests that sympatric species of the genus might show similar dietary compositions, as has been reported for other sympatric anuran species (Sabagh et al., 2012; Oliveira et al., 2015). However, we expect to find differences in dietary composition, as this would enable their sympatry by way of low trophic niche overlap.

MATERIALS AND METHODS

Study site

Our study encompassed nine cattle ranches (Table 1) located in the municipalities of Silvânia and Leopoldo Bulhões, central Goiás state, central Brazil (Fig. 1). The ranches are characterized by Cerrado sensu lato physiognomies (*campo limpo,* areas without shrubs or trees; *campo sujo,* areas with scattered small trees and shrubs; Oliveira-Filho and Ratter, 2002) surrounded by extensive pasture areas. We surveyed one water body per ranch, totalling nine water bodies (Fig. 2), which were selected due to the sympatric occurrence of *Physalaemus cuvieri* and *P. atim* in those locations.

Table 1. Surveyed water bodies in nine cattle ranches in the municipalities of Silvânia and Leopoldo Bulhões, Goiás state, central Brazil.

Survey points	Geographic coordinates
1	16°34′23.8″S, 48°57′16.5″W
2	16°33′59.7″S, 48°55′53.7″W
3	16°35′55.3″S, 48°52′43.8″W
4	16°32′21.4″S, 48°57′48.2″W
5	16°37′45.8″S, 48°47′54.5″W
6	16°34′40.2″S, 48°56′00.9″W
7	16°42′54.4″S, 48°49′44.5″W
8	16°40′15.4″S, 48°50′55.4″W
9	16°39′22.7″S, 48°49′23.5″W

DATA COLLECTION

We conducted 29 expeditions between December 2013 and February 2014 during the breeding season of most anuran species of the region, using randomized order to avoid temporal pseudoreplication. Nocturnal surveys (18:00–00:00) were performed through visual and auditory searching (Scott and Woodward, 1994) to detect *Physalaemus cuvieri* and *P. atim* individuals (Fig. 3).

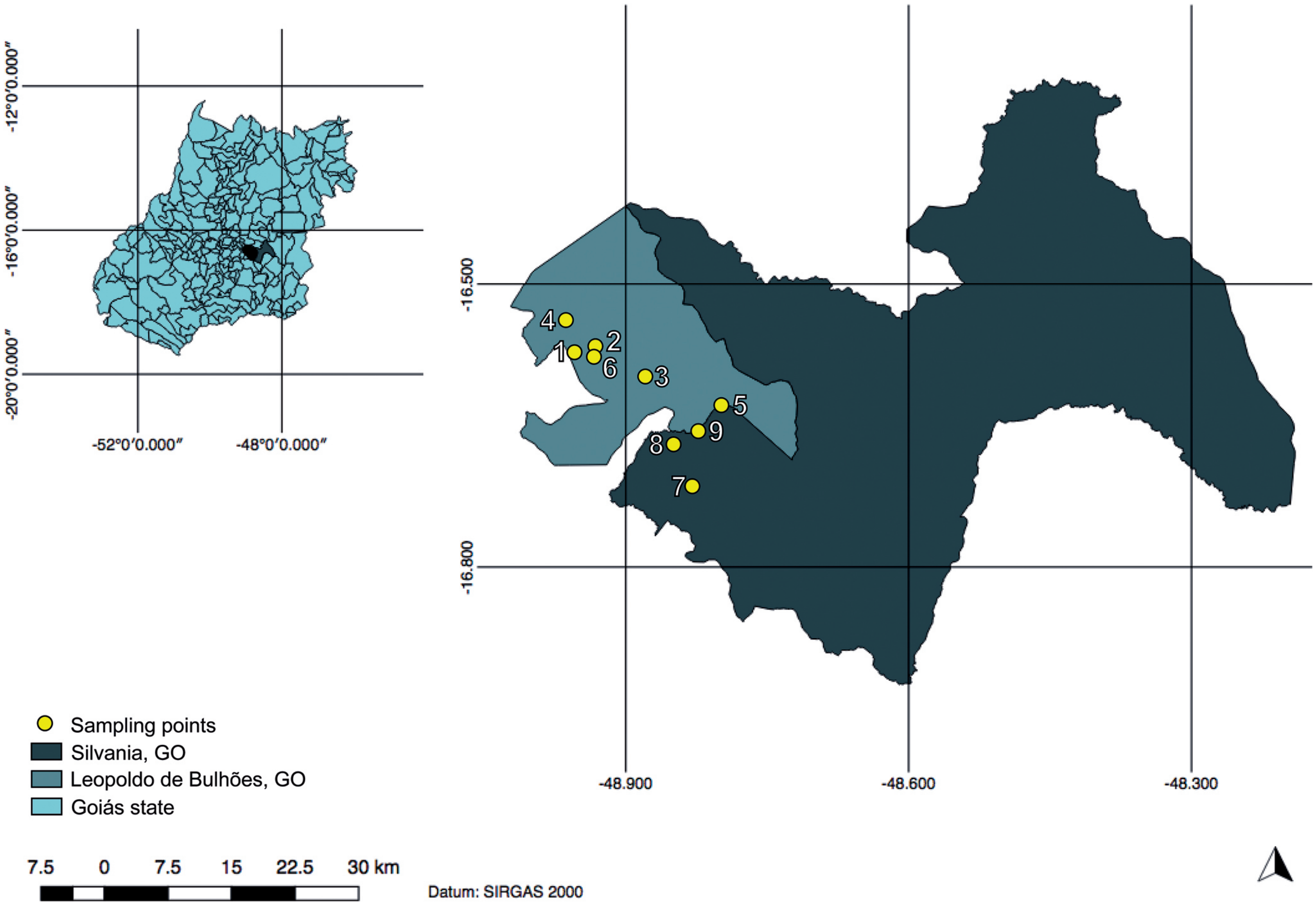

Figure 1. Map of the study sites. Distribution of the surveyed water bodies (survey points) in nine cattle ranches in the municipalities of Silvânia and Leopoldo Bulhões, Goiás state, central Brazil. See general views of the surveyed water bodies in Figure 2.

The stomach-flushing method (Solé et al., 2005) was employed to obtain each individual's stomach contents, and all retrieved food items were preserved in 70% ethanol (Luna, 2005). To avoid flushing the same frog more than once, all individuals were marked using fluorescent alphanumeric labels inserted into the subcutaneous inter-femoral lymph sacs (Clemas et al., 2009). Voucher specimens were deposited in the Coleção Zoológica da Universidade Federal de Goiás (*Physalaemus atim:* ZUFG 8497–8500; *P. cuvieri:* ZUFG 8504–8512).

We performed the following laboratory procedures: stomach content analysis with the aid of a stereomicroscope (Resh and Cardé, 2003); diet analysis based on occurrence, number, and volume per prey category identified to order or family; prey category measurement, expressed as the total volume percentage through the volumetric method (Hyslop, 1980) using a glass counting plate (Hellawell and Abel, 1971); incidence calculation according to the frequency of occurrence of each prey catagory per individual of each species. In addition, we obtained the volume of each item in mm^3 using a milimiter plate for subsequent transformation into mL (Hellawell and Abel, 1971). Preys, especially insects, were highly digestible, because of this we didn't weigh or count the items.

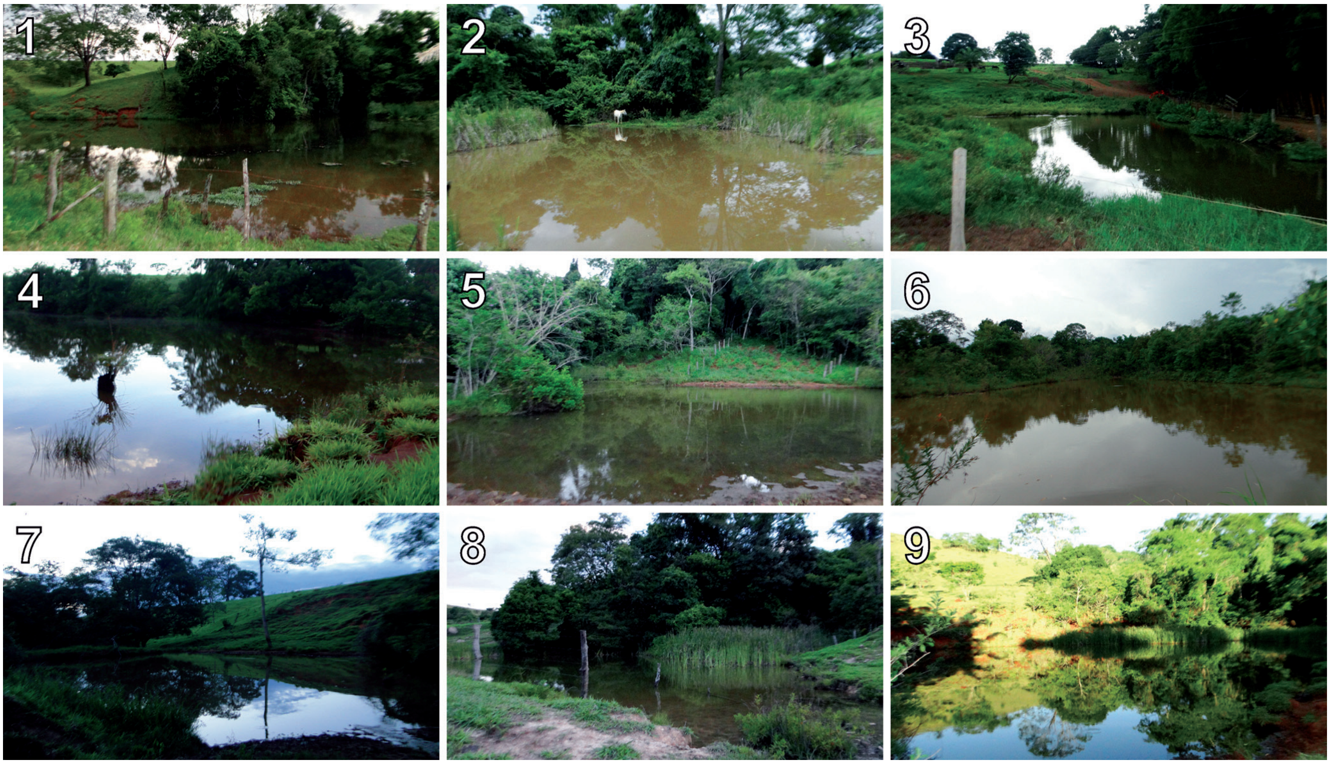

Figure 2. General views of the surveyed water bodies (survey points) in nine cattle ranches in the municipalities of Silvânia and Leopoldo Bulhões, Goiás state, central Brazil. See geographic coordinates of the survey points in Table 1.

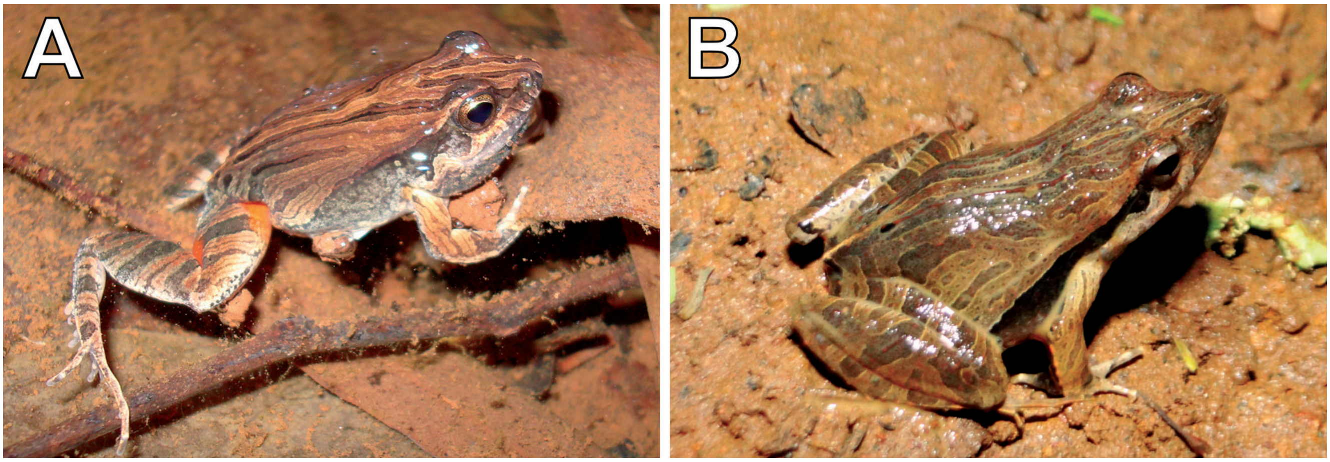

Figure 3. Sympatric specimens of *Physalaemus cuvieri* **(A)** and *P. atim* **(B).**

Data analysis

We calculated the feeding index (IAi; Kawakami and Vazzoler, 1980) to assess each species' diet on the basis of the total volume and occurrence frequency per food item according to the following equation:

$$\mathrm{IAi} = \left[\frac{(\mathrm{FO_i} \times \mathrm{VO_i})}{\sum (\mathrm{FO_i} \times \mathrm{VO_i})}\right] * 100,$$

where IAi is the feeding index, FO is occurrence frequency expressed as a percentage, VO is volumetric frequency expressed as a proportion, and i is the number of food items. We performed a detrended correspondence analysis (DCA; Gauch Jr., 1982) to identify gradients in food item composition as well as a multi-response permutation procedure (MRPP) to compare the diet compositions of *Physalaemus cuvieri* and *P. atim*. All analyses were carried out using the PC-ORD software for Windows, Version 5 (MacCune and Mefford, 1999).

We calculated Levins' Index (Levins, 1968) to determine trophic niche amplitude according to the following equation:

$$\mathrm{B} = \frac{1}{\sum \mathrm{Pi}^2},$$

where B is the trophic niche amplitude value and Pi is the proportion of item i volume for a species. At least two variables with values above 2.36 indicates generalist species (Rossa-Feres and Jim, 2001). We calculated the Trophic Niche Overlap index of Pianka (O_{jk}; Pianka, 1973) to determine trophic niche overlaps between two species based on degree of similarity, according to the following equation:

$$O_{jk} = \frac{\sum_{n=1}^{0} p_{ij} \times p_{ik}}{\sqrt{\sum_{n=1}^{0} p_{ij}^2 \times \sum_{n=1}^{0} p_{ik}^2}}$$

where O_{jk} is the niche overlap index between species j and k; p_{ij} and p_{ik} are the proportions of prey categories consumed by the species; and j, k, and n are the total number of resource categories consumed by species j and k. Index ranged from 0 to 1, in which values equal to zero indicate absence of overlap, and values equal to 1 point out to a complete overlap between species' diets (Krebs, 1999). This analysis was performed using EcoSim Version 7.71 (Gotelli and Entsminger, 2012).

RESULTS

We examined 67 *Physalaemus cuvieri* specimens, among which 53 individuals (79%) had stomach contents, as well as 58 *P. atim* specimens (Table 2), including 45 individuals (78%) with stomach contents (Table 2).

We identified 11 prey categories for *Physalaemus cuvieri* and 17 for *P. atim* (Table 2). Except for Vespoidea Latreille 1802 all prey categories found in *P. cuvieri* were also recorded in *P. atim*. Preys consumed exclusively by *P. atim* included larvae of Coleoptera Linnaeus, 1758, Diptera Linnaeus, 1758, and Lepidoptera Linnaeus, 1758 as well as adults of Blattaria Burmeister, 1829, Collembola Lubbock, 1873, and Gastropoda Cuvier, 1795. Addicionally, we found an aquatic invertebrate (Bryozoa Ehrenber, 1831) as prey of *P. atim* (Table 2). Isoptera Brullé, 1832, Formicidae Latreille, 1809, and Coleoptera were the most numerous and frequent prey in *P. cuvieri,* as were Formicidae, Isoptera, and Aranae Clerck, 1757 for *P. atim* (Table 2). Plant material (i.e., fragments of leaves, twigs, and seeds) were found in the stomachs of 36 *P. cuvieri* specimens (68%) and 26 *P. atim* individuals (58%).

Isoptera had the highest proportional volume in the stomachs of individuals of both frog species. The mean volume of preys ingested per *Physalaemus cuvieri* individual was 12.73 mL, whereas that for *P. atim* specimens was 9.38 mL. No difference in the mean volume of preys per stomach was found between *P. cuvieri* and *P. atim* ($F_{(1.96)}$ = 1.03; *P* = 0.31). Isoptera was the most important prey category for both frog species (*P. cuvieri,* IAi = 86.74; *P. atim,* IAi = 56.47), followed by plant material (*P. cuvieri,* IAi = 8.48; *P. atim,* IAi = 8.71). Formicidae (IAi = 3.38) and Homoptera (IAi = 8.60; Table 2) were the third most important prey category for *P. cuvieri* and *P. atim,* respectively.

The DCA score distribution showed that *Physalaemus atim* has greater diet breadth than *P. cuvieri,* which is consistent with a higher trophic niche breadth in *P. atim* (B = 4.63) than *P. cuvieri* (B = 1.30). According to the MRPP analysis, *P. cuvieri* and *P. atim* have different diet compositions. Nevertheless, the Trophic Niche Overlap index of Pianka revealed high niche overlap between both species (O_{jk} = 88.28%).

DISCUSSION

The number of prey categories consumed by *Physalaemus cuvieri* and *P. atim* was similar to that reported for congenerics, ranging from 12–20 prey categories (Araújo et al., 2009; Rodrigues and Santos-Costa, 2014; Oliveira et al., 2015; Farina et al., 2018). We found *P. cuvieri* individuals to consume fewer prey categories than individuals collected in a remnant of original Cerrado vegetation (shrubby grassland areas) surrounded by wet areas in the municipality of Uberlândia, Minas Gerais state (Araújo et al., 2009). We also found *P. cuvieri* individuals to consume more prey categories than individuals collected in three agroecosystems and forest remnants in the

Table 2. Prey categories consumed by sympatric specimens of *Physalaemus cuvieri* and *Physalaemus atim* surveyed in water bodies in nine cattle ranches in the municipalities of Silvânia and Leopoldo Bulhões, Goiás state, central Brazil. FO, percentage of frequency of occurrence; V, volume percentage of each prey category; IAi, feeding index.

Prey categories	*Physalaemus cuvieri*			*Physalaemus atim*		
	FO (%)	V (%)	IRI	FO (%)	V (%)	IRI
BRYOZOA Ehrenberg, 1831	-	-	-	1 (0.80)	0.01 (< 0.01)	0.01
ARTHROPODA Siebold, 1848						
Myriapoda Latreille, 1802						
Chilopoda Latreille, 1817	2 (1.57)	1.5 (0.14)	0.01	1 (0.80)	1 (0.14)	0.01
Hexapoda Latreille, 1825						
Collembola Lubbock, 1873	-	-	-	1 (0.80)	0.25 (0.03)	0.01
Insecta Linnaeus, 1758						
Blattaria Burmeister, 1829	-	-	-	2 (1.60)	38 (5.45)	0.98
Isoptera Brullé, 1832	33 (25.98)	895.63 (81.13)	86.74	16 (12.80)	272.9 (40.63)	56.47
Coleoptera Linnaeus, 1758	10 (7.87)	31.8 (2.88)	0.93	3 (2.40)	8 (1.19)	0.31
Coleoptera (larvae) Linnaeus, 1758	-	-	-	4 (3.20)	27.8 (4.13)	1.43
Diptera Linnaeus, 1758	5 (3.94)	9.05 (0.82)		9 (7.20)	18.2 (2.70)	2.11
Diptera (larvae) Linnaeus, 1758	-	-	-	6 (4.80)	8.96 (1.33)	0.69
Hymenoptera Linnaeus, 1758						
Vespoidea Latreille 1802	1 (0.79)	3 (0.27)	0.01	-	-	-
Formicidae Latreille, 1809	24 (18.90)	48.02 (4.35)	3.38	17 (13.60)	23.88 (3.55)	5.25
Lepidoptera (larvae) Linnaeus, 1758	-	-	-	4 (3.20)	84 (12.51)	4.35
Hemiptera Linnaeus, 1758	5 (3.94)	1.93 (0.17)	0.01	8 (6.40)	49.5 (7.37)	5.12
Homoptera Boisduval, 1829	2 (1.58)	2.4 (0.22)	0.03	7 (5.60)	95 (14.14)	8.6
Orthoptera Oliver, 1789	3 (2.36)	11 (1.00)	0.10	2 (1.60)	5 (0.74)	0.12
Arachnida Cuvier, 1812						
Araneae Clerck, 1757	3 (2.36)	14.33 (1.30)	0.12	13 (10.40)	32.49 (4.84)	5.43
Acari Leach, 1817	3 (2.36)	5 (0.45)	0.04	1 (0.80)	0.2 (0.03)	0.01
MOLLUSCA Linnaeus, 1758						
Gastropoda Cuvier, 1795	-	-	-	4 (3.20)	6.4 (0.95)	0.33
EXTRA CATEGORY						
Plant material	36 (28.34)	80.28 (7.27)	8.48	26 (20.80)	25.9 (3.71)	8.71
Total		1103.94			697.49	

municipalities of Jaboticabal and Guaíra, São Paulo state (Menin et al., 2015) and in disturbed areas within the Araucaria Forest in the municipality of Campina Grande do Sul, Paraná state (Leivas et al., 2018). These differences are due to variation in prey availability in different habitats (Born et al., 2010; Caldart et al., 2012), which regulates the dietary plasticity in *P. cuvieri* populations at different localities.

It is worth emphasizing that even though most amphibians are predators, plant material is commonly found in the stomach contents of anurans (Kovács et al., 2007; Solé and Pelz, 2007). We also found the stomach content of both *Physalaemus cuvieri* and *P. atim* to contain plant material, probably ingested accidentally, as reported in previous studies on anurans (Protázio et al., 2015; Vogt et al., 2017). Anderson et al. (1999) concluded that the main functions of plant ingestion in anurans include facilitating insect exoskeleton digestion and parasite elimination and providing water to prevent dehydration. We suggest further behavioral studies to understand how *Physalaemus* species feed on termites and ants in the leaf litter and determine if ingestion of leaves is intencional or accidental, and analysis of stable isotopes (e.g., Molina-Burgos et al., 2018) would help determine if ingested plant material is assimilated.

Termites and ants have been considered major food items in several anuran species (Forti et al., 2011; Caldart et al., 2012; Oliveira et al., 2015), and also in the diet of *Physalaemus* species in other regions of Brazil (Santos et al., 2004; Oliveira et al., 2015). Their great importance in both *Physalaemus cuvieri* and *P. atim* suggests that these species forage actively and opportunistically by consuming small preys largely available in the environment (Toft, 1981; Solé and Rödder, 2009). Here, *Physalaemus* species showed preferences for ants, as reported previously for species of this genus, including *P. ephippfer* (Steindachner, 1864) (Rodrigues and Santos-Costa, 2014), *Physalaemus gracilis* (Boulenger, 1883), *Physalaemus biligonigerus* (Cope, 1861) (Oliveira et al., 2015), and *P. cuvieri* (Santos et al., 2004).

According to Clarke (1974), the prevalence of these food items is due to their abundants in the environment and exploitation by few predators. Although the majority of *Physalaemus* food items were terrestrial invertebrates, we identified Bryozoa (aquatic invertebrate) as a prey of *Physalaemus atim*. Cogălniceanu et al. (2000) found aquatic organisms as prey items in the *Pelophylax esculenta* complex. Probably this occurs because the frogs inhabit aquatic environments during reproductive periods.

Aposematic coloration in some frogs is associated with alkaloid toxins accumulated in their skins, derived from the consumption of leaf-litter arthropods, especially ants (Saporito et al., 2004). For *Physalaemus cuvieri,* aposematic coloration appears in the inguinal region, displaying a reddish or orange color pattern. However, there is no evidence that the alkaloid sequestration process occurs in *Physalaemus* species (Moser et al., 2017). Also, aposematic coloration is associated especially to predators-preys interactions.

High diet overlap also has been reported in *Physalaemus* species in sympatry (e.g., Sabagh et al., 2012; Moser et al., 2017). In this study, both *Physalaemus atim* and *P. cuvieri* had high diet overlap since termites are highly important in their diet compositions. However, we found variation in food item composition expressed by MRPP analyses, which might be related to their different body sizes and food resource availability, considering that food resource availability determines the diet of opportunistic species (Sabagh et al., 2012). Moser et al. (2017) performed their study in a subtemperate forest and Sabagh et al. (2012) carried out theirs in a forested area in central Amazonia, both of which have different resource food availability than Cerrado.

Variation of food item compositon is reinforced by niche differentiation, indicating that the sympatric occurrence of *P. atim* and *P. cuvieri* is driven by limiting environmental conditions required for their coexistence in the surveyed habitat (MacArthur and Levins, 1967). Futhermore, the surveyed locations indicate that *P. atim* is a more generalist predator than *P. cuvieri,* which suggests food as a non-limiting factor.

Prey category exclusiveness in sympatric species might be related to differences in foraging behavior (Oliveira et al., 2015) because of trade-offs that can force species to segregate throughout niche dimensions (McPeek, 1996) or food-avoidance to avoid competition (Durbin and Durbin, 1975). Therefore, despite their high overlap, the two species share only a few food items, which differentiates them in the habitat. Shared consumption of other items probably occurs because these preys are abundant in the environment (Pianka, 1974).

In conclusion, *Physalaemus atim* has higher niche amplitude than *P. cuvieri* and, consequently, a more generalist diet. Despite their different sizes, high niche overlap occurred between the species; however, they differed in composition, which ensures a degree of segregation in their sympatric environment. These differences can occur due to different microhabitats being used by each species (Moser et al., 2017). Moreover, other niche dimensions could also be explored to explain the coexistence of these two species, not mediated by their differentiation, but by their similarity, which prevents interspecific competition (Mandai, 2014). Further studies on anuran diet are essential to delimit behavior patterns, such as foraging, and achieve a better understanding of the importance of different food items for each species, as well as to test pertinent ecological hypotheses.

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REFERENCES

Anderson A.M., Haukos D.A., Anderson J.T. 1999. Diet composition of three anurans from the Playa Wetlands of Northwest Texas. *Copeia* 1999:515–520. DOI

Araújo M.S., Bolnick D.I., Martinelli L.A., Giaretta A.A., dos Reis S.F. 2009. Individual-level diet variation in four species of Brazilian frogs. *Journal of Animal Ecology* 78:848–856. DOI

Becker C.G., Joner F., Fonseca C.R. 2007. Ecologically-sustainable tree monocultures contribute to conservation of an Araucaria Forest endemic frog. *Journal of Natural History* 41:1739–1752. DOI

Boisduval J.A. 1829. Essai sur une monographie des zygénides, suivi du tableau méthodique, des lépidoptères d'Europe. Méquignon-Marvis, Paris. DOI

Born M., Bongers F., Poelman E.H., Sterck F.J. 2010. Dry-season retreat and dietary shift of the dart-poison frog *Dendrobates tinctorius* (Anura: Dendrobatidae). *Phyllomedusa* 9:37–52. DOI

Boulenger G.A. 1883. Notes on little-known species of frogs. *Annals and Magazine of Natural History, Series 5* 11:16–19. DOI

Brasileiro C.A., Haddad C.F.C. 2015. A new species of *Physalaemus* from Central Brazil (Anura: Leptodactylidae). *Herpetologica* 71:280–288. DOI

Brullé G.A. 1832. Expédition Scientifique de Morée. Section des Sciences Physiques. Tome III. Partie 1. Zoologie. Deuxième Section–Des Animaux Articulés. Levrault, Paris.

Burmeister H. 1829. De Insectorum systemate naturali. Dissertatio inauguralis. Halis Saxonum, Typis Grunertorum Patris Filiique. DOI

Caldart V.M., Iop S., Bertaso T.R.N., Cechin S.Z. 2012. Feeding ecology of *Crossodactylus schmidti* (Anura: Hylodidae) in southern Brazil. *Zoological Studies* 51:484–493.

Clarke R.D. 1974. Food habits of toads, genus Bufo (Amphibia: Bufonidae). *American Midland Naturalist* 91:140–147. DOI

Clerck C. 1757. Svenska spindlar, uti sina hufvud-slâgter indelte samt under nâgra och sextio särskildte arter beskrefne och med illuminerade figurer uplyste. Stockholmiae, Literis Laur. Salvii. DOI

Clemas R.J., Germano J.M., Peare R.S., Bishop P.J. 2009. Use of three individual marking methods in Australian frogs (genus: *Litoria*) with notes on placement of visible implant alphanumeric tags. *New Zealand Natural Sciences* 34:1–7.

Cogălniceanu D., Palmer M.W., Ciubuc C. 2000. Feeding in anuran communities on islands in the Danube floodplain. *Amphibia–Reptilia* 22:1–19.

Cope E.D. 1861. Descriptions of new species of the reptilian genera *Hyperolius, Liuperus* and *Tropidodipsas. Proceedings of the Academy of Natural Sciences of Philadelphia* 12:517–518.

Cuvier G. 1795. Second mémoire sur l'organisation et les rapports des animaux à sang blanc, dans lequel on traite de la structure des Mollusques et de leur division en ordres, lu à la Société d'histoire naturelle de Paris, le 11 prairial an troisième. *Magazin Encyclopédique, ou Journal des Sciences, des Lettres et des Arts* 2:433–449.

Cuvier G. 1812. Recherches sur les ossemens fossiles de quadrupèdes: où l'on rétablit les caractères de plusieurs espèces d'animaux que les révolutions du globe paroissent avoir détruites. Deterville, Paris. DOI

de Paula-Lima J.E., Rödder D., Solé M. 2010. Diet of two sympatric *Phyllomedusa* (Anura: Hylidae) species from a cacao plantation in southern Bahia, Brazil. *North-West Journal of Zoology* 6:13–24.

Durbin A.G., Durbin E.G. 1975. Grazing rates of the Atlantic menhaden *Brevoortia tyrannus* as a function of particle size and concentration. *Marine Biology* 33:265–277. DOI

Ehrenberg C.G. 1831. Symbolae Physicae, seu Icones et descriptiones Corporum Naturalium novorum aut minus cognitorum, quae ex itineribus per Libyam, Aegyptum, Nubiam, Dongalam, Syriam, Arabiam et Habessiniam Ellipsis studio annis 1820–25 redirerunt. Pars Zoologica, Animalis Evertebrata exclusis Insectis. Officina Academica, Berolini.

Farina R.K., Moser C.F., Witt P., Oliveira M., Tozetti A.M. 2018. Diet of *Physalaemus henselii* (Peters, 1872) (Anura, Leptodactylidae) in southern Brazil. *Herpetology Notes* 11:1001–1002.

Fitzinger L.J. 1826. Neue Classification der Reptilien nach ihren natürlichen Verwandtschaften. Nebst einer Verwandtschaftstafel und einem Verzeichnisse der Reptilien-Sammlung des K.K. Zoologischen Museums zu Wien. J.G. Heubner, Wien. DOI

Forti L.R., Tissiani A.S.O., Mott T., Strüssmann C. 2011. Diet of *Ameerega braccata* (Steindachner, 1864) (Anura: Dendrobatidae) from Chapada dos Guimarães and Cuiabá, Mato Grosso State, Brazil. *Brazilian Journal of Biology* 71:189–196. DOI

Frost D.R. 2020. Amphibian species of the world: an online reference. Version 6.0 (2 June 2020). Accessible at http://research.amnh.org/vz/herpetology/amphibia.

Gauch H.G. Jr. 1982. Multivariate Analysis and Community Structure. Cambridge University Press, Cambridge.

Gotelli N.J., Entsminger G.L. 2012. EcoSim 7.72. Acquired Intelligence, Inc. Accessible at www.uvm.edu/~ngotelli/EcoSim/EcoSim.html. Accessed: 05 October 2015.

Hellawell J.M., Abel R. 1971. A rapid volumetric method for the analysis of the food of fishes. *Journal of Fish Biology* 3:29–37. DOI

Hyslop E.J. 1980. Stomach contents analysis—a review of methods and their application. *Journal of Fish Biology* 17:411–429. DOI

Kawakami E., Vazzoler G. 1980. Método gráfico e estimativa de índice alimentar aplicado no estudo de alimentação de peixes. *Boletim do Instituto Oceanográfico* 29:205–207. DOI

Kovács É.H., Sas I., Covaciu-Marcov S.D., Hartel T., Cupsa D., Groza M. 2007. Seasonal variation in the diet of a population of *Hyla arborea* from Romania. *Amphibia-Reptilia* 28:485–491. DOI

Krebs C.J. 1999. Ecological Methodology. Addison Wesley Educational Publishers, Menlo Park.

Latreille P.A. 1802. Histoire naturelle, générale et particulière des crustacés et des insectes. Ouvrage faisant suite à l'histoire naturelle générale et particulière, composée par Leclerc de Buffon, et rédigée par C.S. Sonnini, membre de plusieurs sociétés savantes. Familles naturelles des genres. Tome troisième, F. Dufart, Paris. DOI

Latreille P.A. 1809. Genera crustaceorum et insectorum secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimis explicata. Tomus quartus et ultimus. A. Koenig, Parisiis. DOI

Latreille P.A. 1817. Les crustacés, les arachnides et les insectes. Pp. 1–653, in Cuvier G. (Ed.), Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Tome III. Deterville, Paris. DOI

Latreille P.A. 1825. Familles naturelles du règne animal, exposées succinctement et dans un ordre analytique, avec l'indication de leurs genres. J.B. Baillière, Paris. DOI

Leach W.E. 1817. The Zoological Miscellany: Being Descriptions of New or Interesting Animals, Vol. 3. E. Nodder & Son, London. DOI

Leibold M.A., McPeek M.A. 2006. Coexistence of the niche and neutral perspectives in community ecology. *Ecology* 87:1399–1410. DOI

Leivas P.T., Leivas F.W.T., Campião K. 2018. Diet and parasites of the anuran *Physalaemus cuvieri* Fitzinger, 1826 (Leiuperidae) from an Atlantic Forest fragment. *Herpetology Notes* 11:109–113.

Levins R. 1968. Evolution in Changing Environments. Princeton Univ. Press, Princeton, N.J. 120 p.

Lima A.P., Magnusson W.E. 1998. Partitioning seasonal time: interactions among size, foraging activity and diet in leaf-litter frogs. *Oecologia* 116:259–266. DOI

Linnaeus C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differential, synonymis, locis, Tomus I. Editio decima, reformata. Laurentiis Salvii, Holmiae. DOI

Lourenço L.B., Targueta C.P., Baldo D., Nascimento J., Garcia P.C.A., Andrade G.V., … Recco-Pimentel S. 2015. Phylogeny of frogs from the genus *Physalaemus* (Anura: Leptodactylidae) inferred from mitochondrial and nuclear gene sequences. *Molecular Phylogenetics and Evolution* 92:204–216. DOI

Lubbock J. 1873. Monograph of the Collembola and Thysanura. Ray Society, London. DOI

Luna J.M. 2005. Técnicas de colecta y preservación de insectos. *Boletín Sociedad Entomológica Aragonesa* 37:385–408.

MacArthur R., Levins R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist* 101:377–385. DOI

MacCune B., Mefford M.J. 1999. PC-ORD: Multivariate analysis of ecological data, Version 6. MjM Software, Gleneden Beach, Oregon. Available from: www.pcord.com/PBooklet.pdf.

Mandai C.Y. 2014. Abordagem teórica na ecologia: uma visão do mundo através de modelos. *Revista da Biologia* 12:1–5. DOI

McPeek M. 1996. Trade-offs, food web structure, and the coexistence of habitat specialists and generalists. *The American Naturalist* 148:124–138. DOI

Menin M., Rossa-Feres D., Giaretta A.A. 2005. Resource use and coexistence of two syntopic hylid frogs (Anura, Hylidae). *Revista Brasilera de Zoologia* 22:61–72. DOI

Menin M., Santos R.S., Borges R.E., Piatti L. 2015. Notes on the diet of seven terrestrial frogs in three agroecosystems and forest remnants in Northwestern São Paulo State, Brazil. *Herpetology Notes* 8:401–405.

Molina-Burgos B.E., Sanchéz A.V., Alvarado-Rybak M., Klarian S., Soto-Azat C. 2018. Trophic ecology of the Endangered Darwin's frog inferred by stable isotopes. *Endangered Species Research* 36:269–278. DOI

Moreira G., Barreto L. 1996. Alimentação e variação sazonal na freqüência de capturas de anuros em duas localidades do Brasil central. *Revista Brasileira de Zoologia* 13:313–320. DOI

Moser C.F., de Avila F.R., de Oliveira M., Tozetti A.M. 2017. Diet composition and trophic niche overlap between two sympatric species of Physalaemus (Anura, Leptodactylidae, Leiuperinae) in a subtemperate forest of southern Brazil. *Herpetology Notes* 10:9–15.

Nascimento L.B., Caramaschi U., Cruz C.A.G. 2005. Taxonomic review of the species group of the genus *Physalaemus* Fitzinger, 1826 with revalidation of the genera *Engystomops* Jimenez-de-la-Espada, 1872 and *Eupemphix* Steindachner, 1836 (Amphibia, Anura, Leptodactylidae). *Arquivos do Museu Nacional* 63:297–320.

Oliveira M., Gottschalk M.S., Loebmann D., Santos M.B., Miranda S., Rosa C., Tozetti A.M. 2015. Diet composition and niche overlap in two sympatric species of *Physalaemus* (Anura, Leptodactylidae, Leiuperinae) in coastal subtemperate wetlands. *Herpetology Notes* 8:173–177.

Oliveira-Filho A.T., Ratter J.A. 2002. Vegetation physiognomies and wood flora of the Cerrado biome. Pp. 91–120, in Oliveira P.S., Marquis R.J. (Eds.), The Cerrado of Brazil. Columbia University Press, New York. DOI

Olivier G.A. 1789. Entomologie, ou Histoire naturelle des insectes, avec leurs caractères génériques et spécifiques, leur description, leur synonymie et leur figure enluminée. Coléoptères. Tome premier. Baudouin, Paris. DOI

Pianka E.R. 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics* 4:53–74. DOI

Pianka E.R. 1974. Evolutionary Ecology. Harper Collins College Publishers, New York.

Protázio A.S., Albuquerque R.L., Falkenberg L.M., Mesquita D.O. 2015. Niche differentiation of an anuran assemblage in temporary ponds in the Brazilian semiarid Caatinga: influence of ecological and historical factors. *Herpetological Journal* 25:109–121.

Resh V.H., Cardé R. 2003. The Encyclopedia of Insects. Academic Press, San Diego.

Rodrigues L.C., Santos-Costa M.C.D. 2014. Trophic ecology of *Physalaemus ephippifer* (Anura: Leptodactylidae) in eastern Amazonia. *Journal of Herpetology* 48:532–536. DOI

Rossa-Feres D.C., Jim J. 2001. Similaridade do sítio de vocalização em uma comunidade de anfíbios anuros na região noroeste do Estado de São Paulo, Brasil. *Revista Brasileira de Zoologia* 18:439–454. DOI

Sabagh L.T., Mello R.S., Rocha C.F.D. 2012. Food niche overlap between two sympatric leaf-litter frog species from Central Amazonia. *Zoologia* 29:95–98. DOI

Santana A.S., Juncá F.A. 2007. Diet of *Physalaemus* cf. *cicada* (Leptodactylidae) and *Bufo granulosus* (Bufonidae) in a semideciduous forest. *Brazilian Journal of Biology* 67:125–131. DOI

Saporito R.A., Garraffo H.M., Donnelly M.A., Edwards A.L., Longino J.T., Daly J.W. 2004. Formicine ants: An arthropod source for the pumiliotoxin alkaloids of dendrobatid poison frogs. *Proceedings of the National Academy of Sciences of the United States of America* 101:8045–8050. DOI

Schoener T.W. 1974. Resource partitioning in ecological communities. *Science* 185:27–39. DOI

Scott N.J. Jr., Woodward B.D. 1994. Standard techniques for inventory and monitoring: Surveys at breeding sites. Pp. 118–125, in Heyer W.R., Donelly M.A., McDiarmid R.W., Hayek L.C., Foster M.S. (Eds.), Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Smithsonian Institution Press, Washington.

Siebold C.T.v. 1848. Lehrbuch der vergleichenden Anatomie der Wirbellosen Thiere. Erster Theil. P. 679, in Siebold C.T.V., Stannius H. (Eds.), Lehrbuch der vergleichenden Anatomie. Verlag von Veit & Comp., Berlin. DOI

Solé M., Pelz B. 2007. Do male tree frogs feed during the breeding season? Stomach flushing of five syntopic hylid species in Rio Grande do Sul, Brazil. *Journal of Natural History* 41:2757–2763. DOI

Solé M., Rödder D. 2009. Dietary assessments of adult amphibians. Pp. 167–184, in Dodd C.K. Jr. (Eds.), Amphibian Ecology and Conservation: A Handbook of Techniques. Oxford University Press, Oxford.

Solé M., Beckmann O., Pelz B., Kwet A., Engels W. 2005. Stomach flushing for diet analysis in anurans: an improved protocol evaluated in a case study in Araucaria forests, southern Brazil. *Studies on Neotropical Fauna and Environment* 40:23–28. DOI

Steindachner F. 1864. Batrachologische Mittheilungen. *Verhandlungen des Zoologisch-Botanischen Vereins in Wien* 14:239–288.

Toft C.A. 1981. Feeding ecology of Panamanian litter anurans: patterns in diet and foraging mode. *Journal of Herpetology* 15:139–144. DOI

Vogt S., Villiers F.A., Ihlow F., Rödder D., Measey J. 2017. Competition and feeding ecology in two sympatric *Xenopus* species (Anura: Pipidae). *PeerJ* 5:e3130. DOI

Werner F. 1896. Beiträge zur Kenntniss der Reptilien und Batrachier von Centralamerika und Chile, sowie einiger seltenerer Schlangenarten. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* 46:344–365.